FINE LITTERFALL AND LEAF DECOMPOSITION
IN A MONTANE KOA-OHIA RAIN FOREST

Paul G. Scowcroft
Pacific Southwest Forest and Range Experiment Station
Forest Service
US Department of Agriculture
1151 Punchbowl St., Rm. 323
Honolulu, Hawaii 96813

Abstract

Nutrients returned to the forest floor in litterfall and release of nutrients during decomposition are important nutrient cycling processes. Both of these ecosystem level processes may be changed by establishment of alien (introduced) plant species in predominantly native communities. Preliminary studies of litterfall and decomposition were done in a montane rainforest on the island of Hawaii to get indications of rates and to refine sampling procedures. Fine litterfall dry mass and nutrient mass were estimated from litter trap collections in two young koa (*Acacia koa*) stands and one old koa-ohia (*Metrosideros polymorpha*) stand in which the alien vine, banana poka (*Passiflora mollisima*), was established. Annual litterfall averaged from 6,300 to 12,200 kg/ha. Litterfall for the two upper elevation stands lies within the range of values reported for several other tropical montane rain forests. Return of nitrogen and phosphorus per unit of leaf litter dry mass were greater in pole-size koa stands than in the mature koa-ohia stand. Decomposition of koa, ohia, and banana poka foliage was studied using litter bags. Sclerophyllous foliage of koa and ohia, the native species, decayed more slowly than the non-sclerophyllous foliage of the alien, banana poka. High nutrient concentrations and low lignin concentrations in poka litter probably account for its rapid decay. Decomposition of the three species of leaf litter was correlated with initial nitrogen concentration. Banana poka litter may speed decomposition of recalcitrant native leaf litter when they occur in mixture.

Introduction

Knowledge of productivity, nutrient cycling, and other functional characteristics of tropical montane forests is limited. Opportunity exists in Hawaii to expand knowledge of these montane ecosystems and at the same time gather information needed to assure the continued existence and functioning of local forests. Such information would promote survival and recovery of endangered native forest birds and plants, and promote maintenance of watershed stability.

Koa (*Acacia koa*) and koa-ohia (*Metrosideros polymorpha*) forests are two of Hawaii's montane forest types. On the island of Hawaii, they occur primarily between 1,200 and 1,800 m elevation. The woody plants and tree fern, which collectively account for most of the plant biomass, are native. Banana poka (*Passiflora mollisima*) is a notable exception.

An aggressive alien vine deliberately introduced from South America, banana poka poses a significant threat to koa and koa-ohia forest on the windward side of the island of Hawaii where climatic and edaphic conditions are ideal for growth of the vine. In forest openings, it covers shrubs, ferns, and low growing trees. Regeneration of koa, ohia, and other species in tree-fall gaps, the primary mechanism of natural forest regeneration, are often covered with the vine. Banana poka is capable of climbing at least 20 m into the crowns of older overstory trees and forming a curtain to the forest floor. The relatively open forest canopy and lack of native lianas also favor growth and spread of banana poka.

Besides affecting structural characteristics of native forest ecosystems, successful establishment of alien species may also affect functional characteristics, such as energy flow, productivity, and nutrient cycling. The flow of nutrients from soil to plant and back to the soil and the various processes regulating the flow are critically important to activity and change in forest ecosystems, so much so that some ecologists consider it the heart of ecosystem dynamics. The introduction and establishment of an aggressive alien plant like banana poka into a tropical montane forest ecosystem has the potential to change established flows.

Recent investigation (Scowcroft, unpublished data) has shown high concentrations of major nutrients in mature foliage and leaf litter of banana poka. Mature leaves averaged 3.6% N, 0.2% P, 1.4% K, 2.0% Ca, and 0.5% Mg on oven-dried basis. Such nutrient concentrations are greater than any native species analyzed. Nutrient uptake by banana poka places an added drain on soil nutrient pools, thus potentially reducing the amounts available for native species. If uptake and immobilization in live alien biomass is great enough, productivity of native species could be adversely affected.

This paper reports preliminary studies of litterfall and decomposition in a mature closed canopy koa-ohia stand and in two young pole-size stands, one adjacent to the mature stand and the other at a lower elevation. Annual litterfall biomass and nutrient masses returning to the forest floor are estimated. Rates of decomposition of koa, ohia, and banana poka leaf litter are estimated. Correlations between decomposition and concentrations of N, P, K, Ca, and Mg in residual material for each type of litter are examined. Based on evaluation of the data and problems encountered in the field, recommendations are made to refine sampling procedures.

Study Sites and Methods

The Laupahoehoe section of the Hilo Forest Reserve was selected for study because it contains both mature and immature stands of trees and because banana poka heavily infests the forest. A 30- by 30-meter plot was established in a mature koa-ohia stand located at 1,460 m elevation. A second and similar plot was established in a nearby pole-size koa stand. A third plot was laid out in another pole-size stand at 1,070 m elevation. Median annual rainfall is 3,200 mm/yr at the upper sites and 5,000mm/yr at the lower site (Division of Water and Land Development 1982). Air temperature is about 5°C warmer at the lower site than at the higher site.

Fine litterfall

I randomly installed four litter traps in the mature stand and three traps in each of the pole-size stands on January 18, 1985. Each trap consisted of a plastic pot, 527 cm^2 at the mouth, with a fiberglass screen suspended 15 cm below the rim to allow free water drainage. Traps were mounted on steel fence posts with leveled rims 1 m above the ground.

Litterfall collections were made periodically for 361 days. Maximum time between collections was 39 days. With the exception of banana poka fruit, which can be 4 cm diameter and 10 cm long, litter caught in the traps was fine litter as defined by Vitousek (1984). We bagged the litter from each trap and oven-dried them at 70°C for 24 hrs. After drying, litter was separated into four categories: (1) foliage, including fern fronds; (2) bark, twigs, and lichen; (3) reproductive parts; and (4) insects, insect frass, and miscellaneous material that could not be tied to another category. Foliage and reproductive parts were segregated further by species. Each component was weighed separately.

Annual returns of nitrogen, phosphorus, and calcium in leaf litter were estimated by multiplying litter dry mass by element concentrations in independently collected samples of koa, ohia, banana poka, tree fern (*Cibotium* sp.), and olapa (*Cheirodendron* sp.) foliage. These five species made up 83% of the foliar litter in the mature stand and 93% and 92% of the foliar litter in the upper and lower pole-size stands, respectively. Nutrient returns reported in this paper probably underestimate actual return because values are based on only part of the total fine litterfall.

Decomposition

I used the litter bag method to study decomposition of koa, ohia, and banana poka leaf litter. Bags were 18 by 20 cm and were made from fiber glass screen with a mesh size of 1 by 2 mm.

Leaf litter for each species was collected from the forest floor and taken to the laboratory where it was air dried over night. Subsamples of the leaves of each species were taken and analyzed for oven-dry mass, moisture content, total nitrogen (micro-Kjeldahl; Technicon Instrument Corp. 1977), and phosphorus, potassium, magnesium, sulfur, and calcium (x-ray fluorescence; Jones and Okazaki 1973). The equivalent of 8 to 10 grams oven dry weight of leaves of a single species were placed into labelled litter bags. On March 21, 1985, I anchored 27 bags of each species to the forest floor with flagged wire pins.

Three randomly selected bags of each species were retrieved monthly for 9 months. After removal of invertebrates, residual materials were analyzed for oven-dry mass and total nitrogen, phosphorus, and calcium.

Loss of mass data were fit to the single exponential decay model:

$$X_t / X_o = e^{-kt}$$

where X_t is the mass of material remaining at time t, X_o is the mass of material at t=0, k is the decay constant, and e is the natural logarithm base.

The relationship between loss of mass and initial nutrient content of foliar litter was examined by linear regression. The relationships between loss of mass and residual nitrogen concentration was examined by linear and curvilinear regression for each species.

Results and Discussion

Fine litterfall

Annual litterfall ranged from 6.3 (±0.9 s.e.) Megagrams(Mg)/ha in the upper-elevation pole-size stand to more than 12.2 (±2.8 s.e.) Mg/ha in the lower-elevation pole-size stand (Fig. 1). Fine litterfall in the mature stand (6.7 ± 2.5 s.e. Mg/ha) was not significant different from litterfall in the young stand nearby (P>0.05).

In general, both upper elevation stands produced less fine litter than several other tropical montane rain forests (Fig. 1). The low elevation koa stand showed much greater litter production than other montane forests and even ranked among the most productive of lowland tropical forests

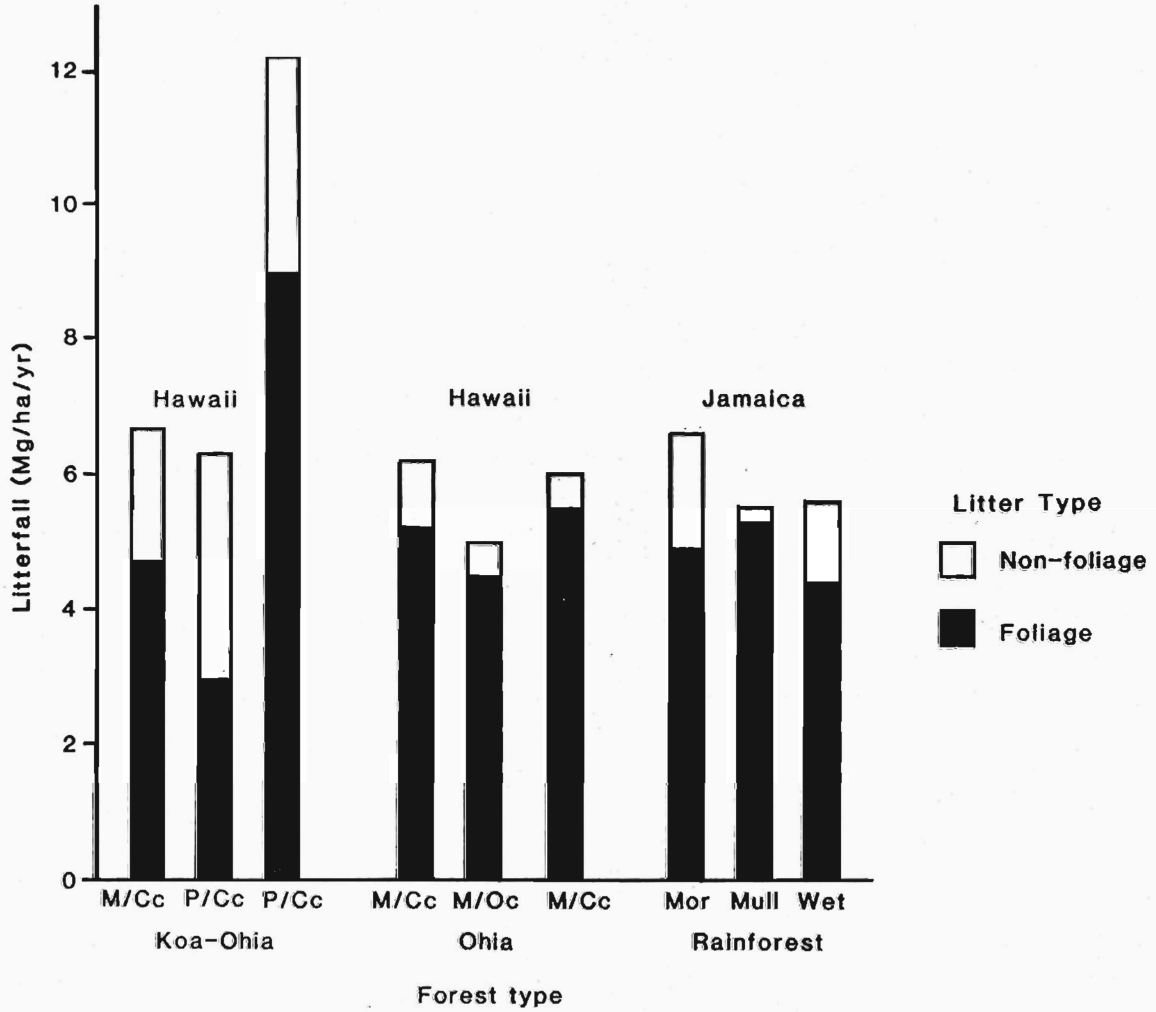

Figure 1. Annual fine litter production in several tropical montane rain forests, by litter type and stand type. (M/Cc = mature, closed canopy; M/Oc = mature, open canopy; P/Cc = pole-size, closed canopy). Sources for data: Ohia--Gerrish and Bridges 1984; Jamaican rainforest--Tanner 1980; Koa-ohia--This study.

(Vitousek 1984). Whether this high litterfall is real or is an artifact of too few traps placed by chance in positions where the catch was high, can not be determined without more intensive sampling.

Foliage accounted for more than 70% of annual litter production in the mature stand and in the young, low elevation stand (Fig. 1). Actual foliage dry mass was 4.7 (±0.5 s.e.) Mg/ha in the mature stand and 9.0 (±1.8 s.e.) Mg/ha in the young, low elevation stand. By contrast, foliage accounted for less than one-half of annual litter production in the young, high elevation stand. Actual foliage dry mass was 3.0 (±0.5 s.e.) Mg/ha.

Compared to other mature montane rain forests in Hawaii and Jamaica, the two upper elevation stands produced less leaf litter, both in terms of absolute amounts and proportion of annual litter production (Fig. 1). In contrast, the low elevation koa stand produced more foliar litter than other Hawaiian or Jamaican forests (Table 1). Production even rivaled that of many lowland tropical rainforests (Vitousek 1984). Climatic differences among forests may explain some of the variation in leaf litter production.

Composition of foliar litter varied among my study sites and reflects overstory species composition. For example, ohia dominated the overstory in the mature stand. Less than 20% of the overstory was koa. Banana poka vines were in the tree canopies, but not in high density. Leaf litter production clearly reflects this overstory composition--68% ohia, 11% koa, and 3% banana poka (Fig. 2).

Green foliar litter, i.e., leaves which appeared to have fallen prematurely, comprised 1 to 3% of the annual leaf litter production at the study sites. Green litter was collected only from January through May. High winds probably caused most of the green litterfall.

Production of fine litter was relatively constant over the year, except for 2 or 3 peaks at each site (Fig. 3). The peaks resulted mainly from too small sample size coupled with infrequent catches of whole banana poka fruit or branch tips snapped off by high winds. I would expect less pronounced peaks with increased sample size, because fruit and twig weights would be averaged over more traps.

Preliminary estimates of annual nutrient return to the forest floor in leaf litter indicate that the upper elevation pole-size stand returned almost as much nitrogen, phosphorus and calcium as did the mature stand nearby (Table 1). Returns in my low elevation stand were more than double those in the higher elevation stands.

Nutrient returns generally lay within the ranges reported for other montane tropical forests (Table 1). However, nitrogen and phosphorus returns for my low elevation stand were well outside reported ranges.

Nutrient concentrations (annual nutrient mass/annual dry mass) were variable. Nitrogen concentration was least for leaf litter in the mature stand (1.17%). Phosphorus concentrations were similar for all three stands--0.10 to 0.11%. Calcium concentration was greatest in the mature stand (0.77%).

Concentrations of nitrogen and phosphorus in leaf litter were greater for the stands I studied than for other montane stands. For example, nitrogen concentration ranged from 1.17 to 1.60% for my stands compared to 0.59 to 0.99% for other stands listed in Table 1. Calcium concentrations lay within the range of values reported for other montane forest.

<u>Decomposition</u>

Koa phyllodes and ohia and banana poka leaves decomposed at different rates (Fig. 4). After 284 days of decomposition, 69% of the dry weight of ohia leaves remained, 36% of the koa phyllodes remained, but none of the

Table 1--Fine litterfall dry mass and nutrient mass in tropical montane rain forests

Location	Lat.	Elev.	Rain	Type	Litterfall: Dry mass	Litterfall: N	Litterfall: P	Litterfall: Ca	Reference
		m	mm		Mg/ha/yr	kg/ha/yr			
Jamaica	18°N	1600	3000	mor ridge	6.6	39	1.3	34	Tanner 1977
	18°N	1600	3000	mull ridge	5.5	49	1.5	50	Tanner 1977
	18°N	1600	3000	wet slope	5.5	34	2.1	53	Tanner 1977
	18°N	1600	3000	gap	6.5	58	2.4	55	Tanner 1977
Hawaii	20°N	1420	3200	ohia	5.2	31	1.7	136	Vitousek 1984
	20°N	1220	3500	ohia	5.2	37	2.1	84	Vitousek 1984
	20°N	1200	2500	ohia	6.3	37	2.1	110	Vitousek 1984
Venezuela	8°N	2250	1500	rain forest	7.0	69	4.0	43	Vitousek 1984
Hawaii	20°N	1500	3200	mature koa-ohia*	4.7	55	4.8	36	Present study
	20°N	1500	3200	pole-size koa*	3.0	48	3.4	33	Present study
	20°N	1100	5000	pole-size koa*	9.0	132	8.9	58	Present study

*Litterfall dry mass in koa and koa-ohia stands includes leaf litter only. Nutrient mass estimates based on mean N, P, and Ca concentrations of koa, ohia, treefern, banana poka, and olapa litter only. The combined litter of these species represented 83% of the leaf litter at site 1, 93% at site 2, and 92% at site 3.

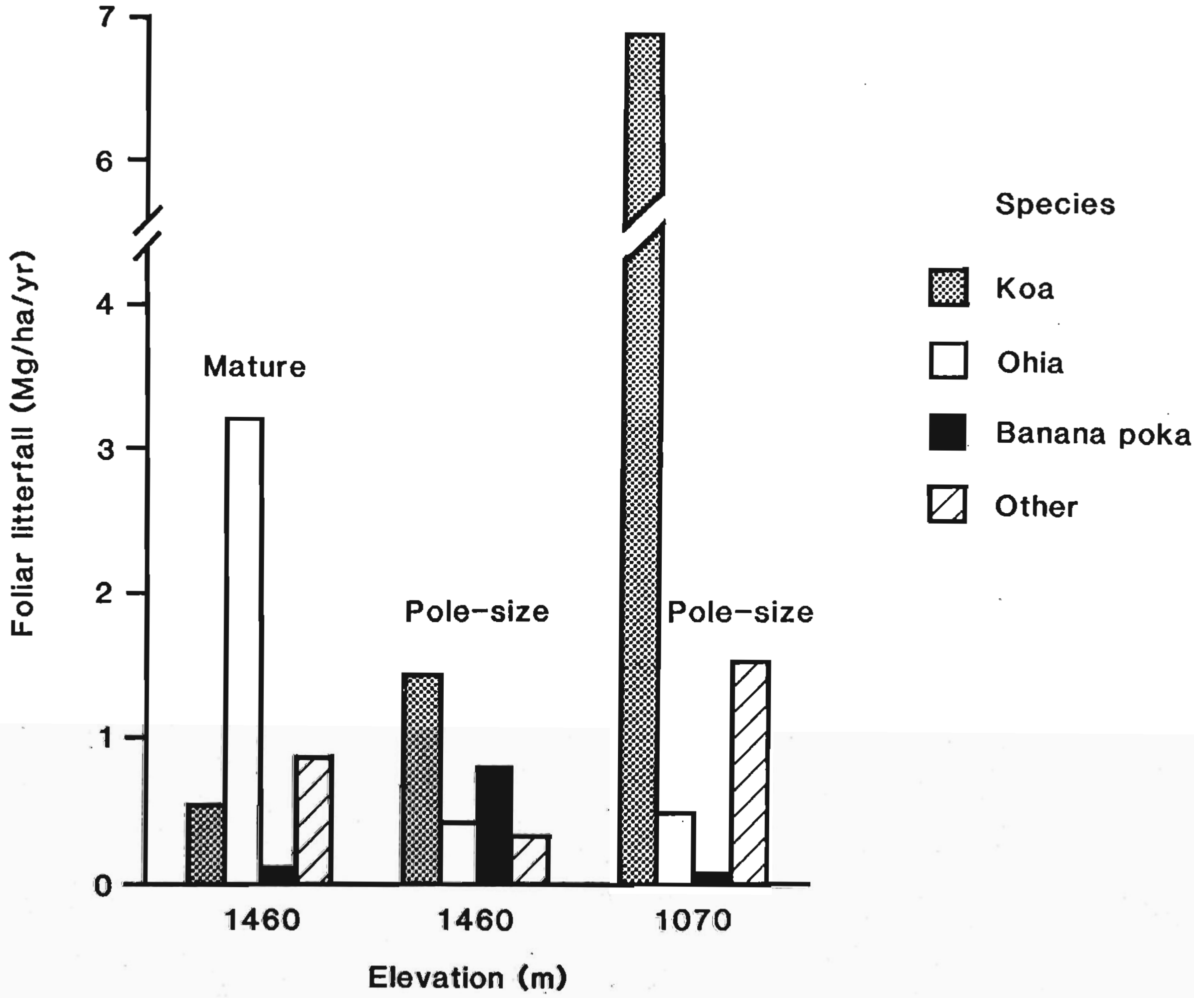

Figure 2. Foliar litter produced annually by mature and pole-size koa-ohia stands in the Laupahoehoe section of the Hilo forest reserve, by species and stand elevation.

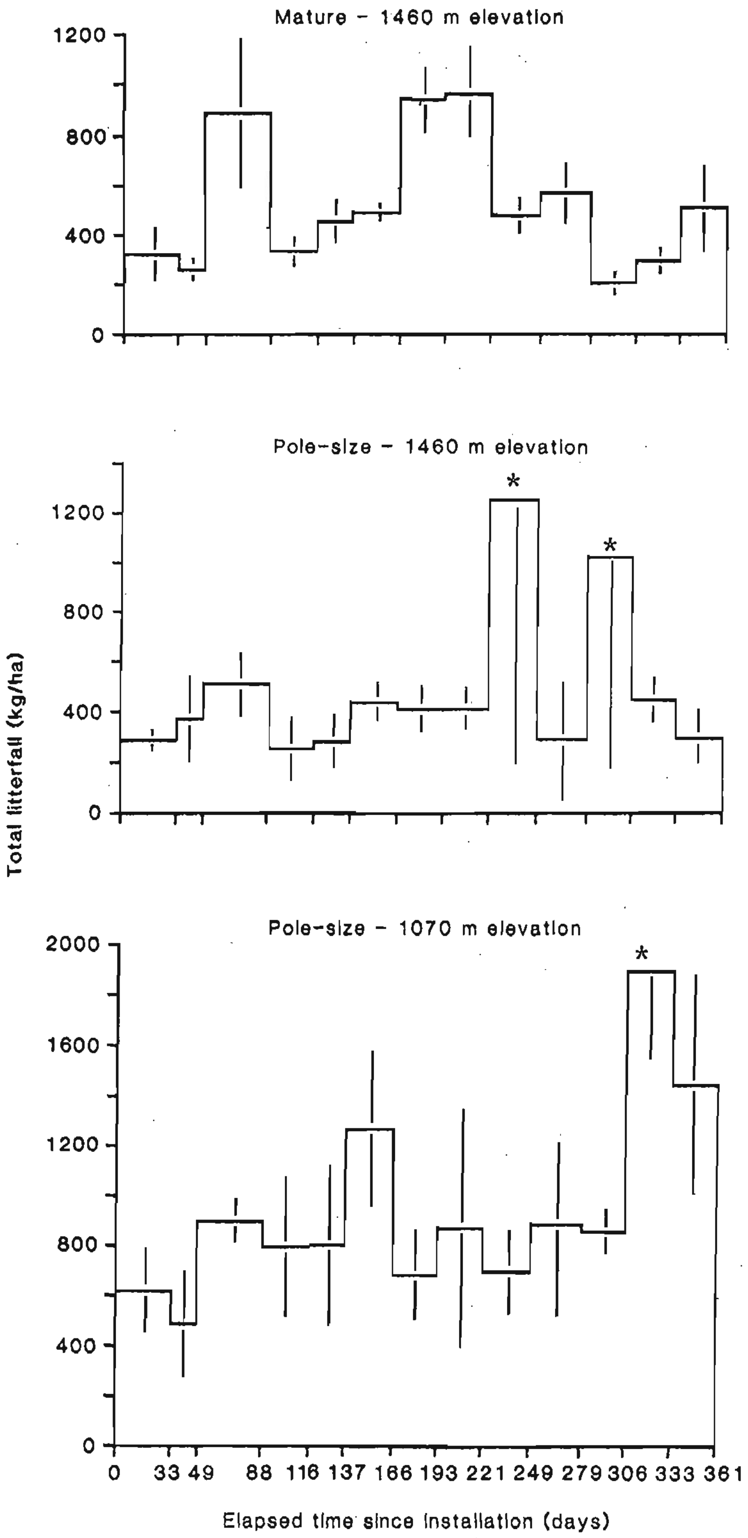

Figure 3. Average periodic fine litterfall in koa-ohia forests, by stand. Vertical bars indicate $\pm$ s.e. (n=3 or 4). Only lower one-half of s.e. bar shown where asterisks occur.

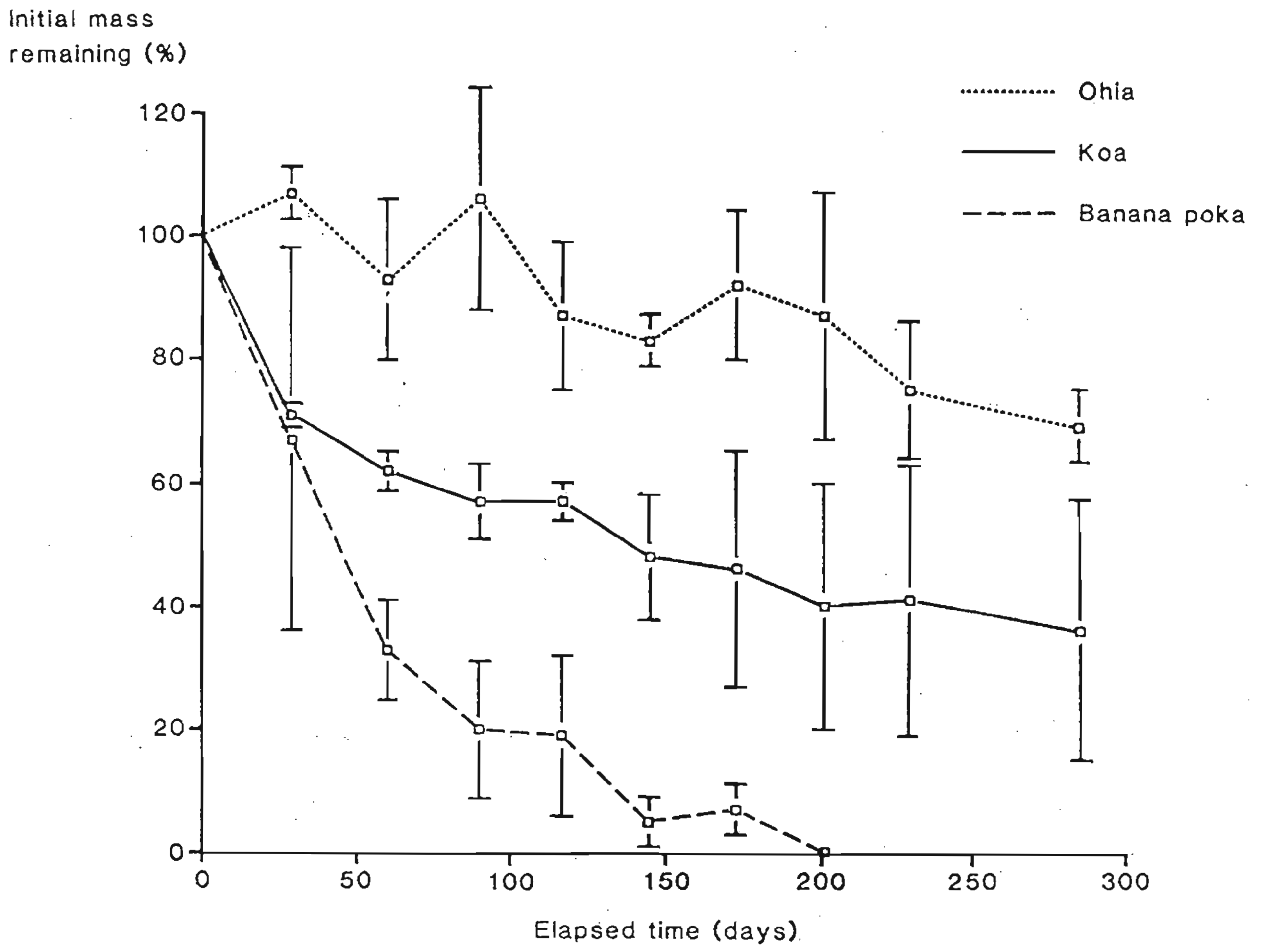

Figure 4. Percentage of initial leaf dry mass remaining after various periods of decomposition, by species. Vertical bars indicate ± s.e. (n = 3).

banana poka leaves remained. In comparison, after 325 days, 15 to 70% of the dry weight of 7 native tree leaf litters remained in a lower montane New Guinea rain forest (Edwards 1977). The dry weight of leaf litter remaining after one year in montane Jamaican rain forests ranged from <4 to 73% for 15 different tree species (Tanner 1981).

Decay constants (k) were 0.37/yr for ohia, 1.73/yr for koa, and 6.57/yr for banana poka. Fitted curves explained 61% of the observed variability for ohia, 81% of the variability for koa, and 91% of the variability for banana poka. Edwards (1977) calculated a k value of 0.63/yr for seven montane tree species. I believe the differences in decay rates are largely a function of chemical quality of the litters.

The inverse of k is the mean residence time of litter on the forest floor. Mean residence time was 2.70 yrs for ohia, 0.58 yrs for koa, and 0.15 yrs for banana poka.

Research with a wide variety of plant detritus has shown that overall rate of disappearance of litter depends on quality of the material, e.g., its organic forms, the concentration of carbon, nitrogen, phosphorus, and other nutrients essential for microbial growth, and the concentrations of potential microbial growth inhibitors (Jensen 1974; Swift et al. 1979). Generally, sugars are degraded most rapidly, followed in order of increasing resistance to decay by hemicellulose, cellulose, lignin, waxes, and phenols (Smith 1982). Thus, forest litter high in lignin, such as bark, decomposes more slowly than litter which is low in lignin, such as leaves (Fogel and Cromack 1977; Melillo et al. 1982). I suspect that decay resistant compounds are most abundant in ohia litter and least abundant in banana poka litter. Additional study on this subject is being planned.

Nutrient content, particularly nitrogen, also correlates with decay rates. Slowest decay occurs in materials that are relatively low in ash and nitrogen and have high C:N ratios (Cromack and Monk 1975; Thaiutsa and Granger 1979). This generalization applied to decomposition of ohia, koa, and banana poka litter (Fig. 5). Ohia litter had the lowest initial nitrogen concentration (1.09%) and it decayed most slowly. Koa litter had 1.66% nitrogen initially and it decayed at an intermediate rate. Banana poka had the highest initial nitrogen concentration (2.19%) and it decayed most rapidly. Initial concentration of other essential nutrients were not as well correlated with decomposition as was nitrogen (Table 2).

Initial potassium content and decay were positively correlated--as potassium concentration increased, decomposition decreased. This relationship may be indicative of susceptibility of different foliar litters to leaching and of relative abundance of structural compounds resistant to microbial attack. Loss of potassium, which is the most leachable element, from sclerophyllous ohia and koa litter may be slowed by cuticular waxes. Banana poka leaves may have little structural protection against potassium leaching.

Decay of some leaf litters is inversely correlated with nitrogen concentration in residual material (Aber and Melillo 1980; McClaugherty et al. 1985). Explanations offered to account for accumulation of nitrogen in decaying plant litter include fixation, fungal translocation, microbial immobilization, throughfall, dryfall, and insect frass (Melillo et al. 1982). For the inverse relationship to exist, three conditions must be met (Aber and Melillo 1980): (1) Physical removal of material from litter bags must be minimal, (2) nitrogen concentration in the litter must be limiting for microbial activity, and (3) a continuous external source of N must be available to the microorganisms.

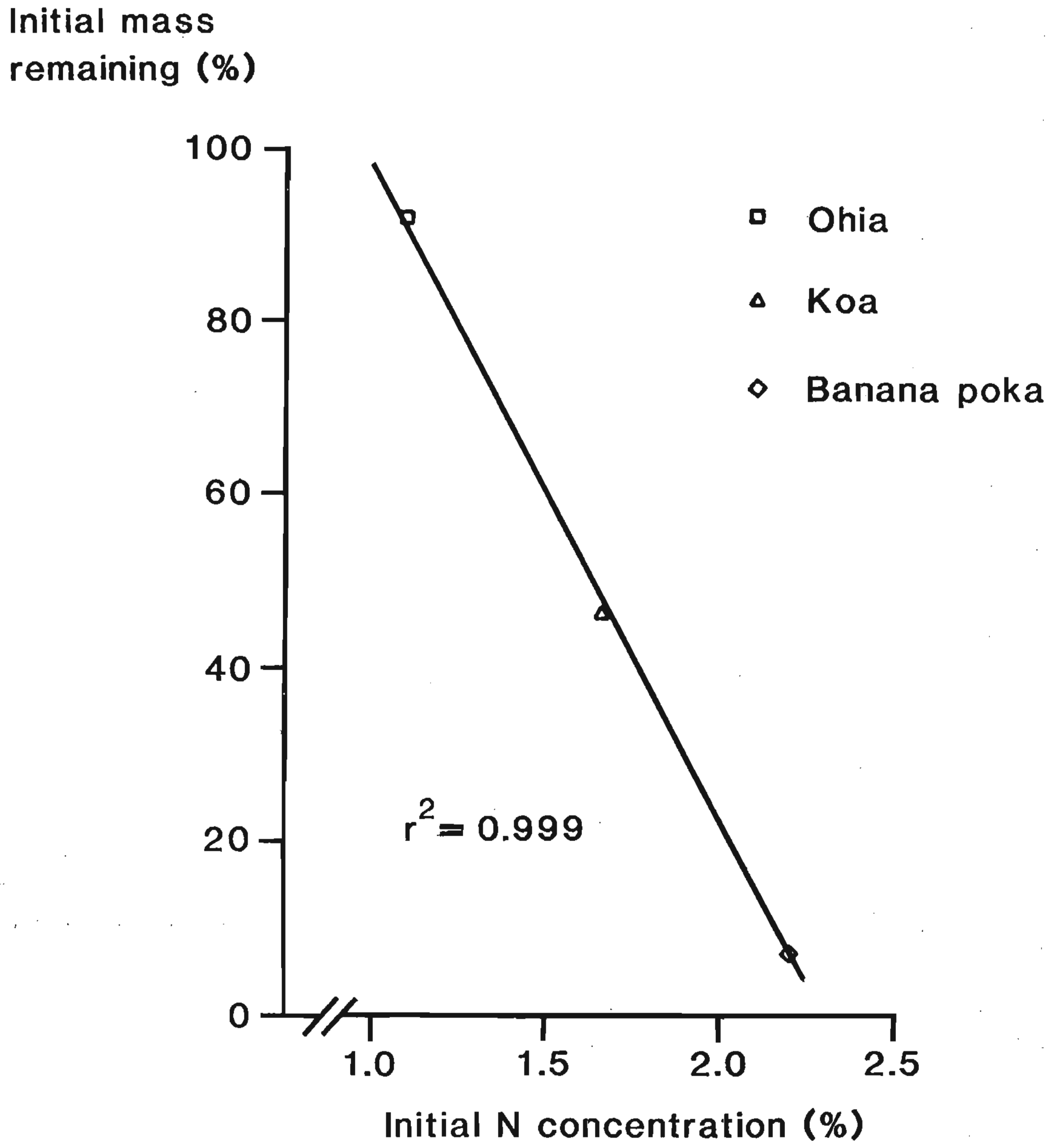

Figure 5. Percentage of initial leaf dry mass remaining after 173 days of decomposition expressed as a function of initial nitrogen concentration.

Table 2--Coefficients of determination (r^2), slopes, and intercepts relating percentage of initial mass remaining after 173 days of decay to initial concentration of various nutrients for ohia, koa, and banana poka leaf litter

Nutrient	(r^2)	Slope	Intercept
N	1.00	-0.77	1.76
P	0.58	-8.57	1.57
K	0.86	3.73	-0.64
Ca	0.71	-0.35	0.91
Mg	0.75	-0.60	0.78
S	0.81	-4.38	1.23

Of the three species I studied, only koa showed a strong inverse relationship (Fig. 6) and the best fit was curvilinear, not linear as reported by others (Aber and Melillo 1980; McClaugherty et al. 1985). One or more of the conditions necessary for a good inverse linear relationship may not have been met in my study. Both koa and banana poka litter had high nitrogen concentrations at the start. Furthermore, earthworms, millipedes, detritus-eating moth larvae, and snails moved in and out of the bags, carrying away ingested material and physically breaking the litter into pieces that could filter out of the bag. The lack of a demonstrable relationship for ohia, which had the lowest nitrogen concentration of the three litters, may be the result of invertebrate activity.

Sample design

This preliminary research revealed several sampling problems for litterfall and decomposition studies. First, more sampling units are needed to make estimates of both litterfall and decomposition more precise. To illustrate, if I wanted to estimate mean annual leaf litter production within ±500 kg/ha and be correct 95% of the time, the preliminary data indicate that I would need 18 traps/plot in the mature stand, 11 traps in the young, upper-elevation stand, and 158 traps in the young, lower-elevation stand. Similarly, if I wanted to separately estimate mean leaf litterfall for koa, ohia, and banana poka within ±10% and be correct 95% of the time, I would need the following number of traps/plot:

	Mature stand	Upper young stand	Lower young stand
Koa	551	39	56
Ohia	17	1084	928
Poka	68	54	1151

Lacking money and time for large sample sizes, the obvious conclusion from these and other calculations (not shown) is that estimates of litterfall and decomposition can not be as precise as I would like.

The second problem, which was related to sample size, was trap size. Tanner (1980) and Edwards (1977) used 1 m^2 traps. Others have used traps as small as 0.01 m^2 (McShane et al. 1983). Trap size should be larger than the largest litter of interest, but not so large that excessive time is spent separating material into components parts. McShane et al. (1983) found that for a given level of precision, the cost of obtaining estimates of conifer needle fall decreased with decreasing collector size, from 0.93 to 0.01 m^2. Trap size in this preliminary study was 0.05 m^2 or 10 times larger than banana poka fruit and 5 times larger than olapa leaves. On the basis of my experience sorting litter and based on findings of McShane et al. (1983), I believe the small traps I used were adequate for most litter collected.

The third sampling problem was how to estimate fine litterfall for tree fern. Small litter traps set at 1 m above ground may not be appropriate for sampling deposition of fronds on the forest floor. Tree fern fronds do not abscise. Even when they fall over under their own weight some months after death, the frond may not touch the forest floor, but instead hang from the tree fern above the forest floor. Technically, such litter best fits the definition of standing detritus and is analogous to dead twigs and branches that remain attached to trees. Only when standing detritus becomes detached does it return to the forest floor. Estimating actual return of tree fern litter to the forest floor may require a combination of techniques including (1) litter traps positioned directly under tree fern coupled with estimates of tree fern density, (2) random string transects to

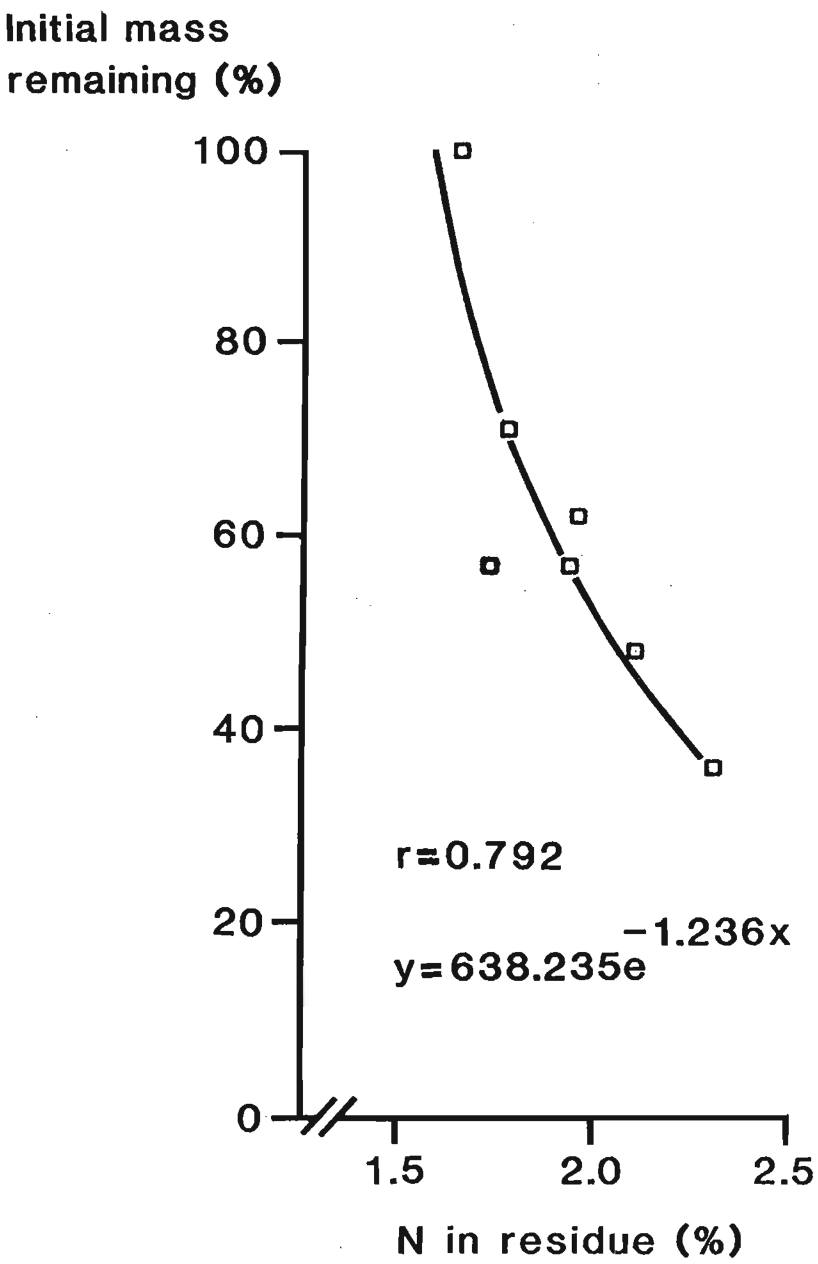

Figure 6. Percentage of initial koa phyllod dry mass remaining expressed as a function of the nitrogen concentration in the residual material.

measure weight of fronds falling on the ground, and (3) large scalped plots that serve as defacto litter traps and would be used to collect tree fern data only.

Finally, the problem of pig disturbance of plots is serious especially for decomposition studies. I found that pigs will trample, eat, and generally wreak havoc on litter bags. Bags that are not destroyed or lost may be heavily contaminated with soil thus making chemical analyses of residual material suspect. The solution is to construct exclosures in which decomposition studies can be done. Fencing increases the cost of studies, but it also increases the likelihood of getting good data. Pig-free sites also can be used to study other processes such as litter accumulation and seedling recruitment.

Conclusions

Banana poka, which was the introduced species in my study plots, comprised a small fraction of annual fine litter production in the mature koa-ohia stand. If this mature stand is typical of other mature portions of the forest, as my observations suggest, then banana poka is having minimal impact on litterfall in those areas. This is not true of young stands where banana poka grows best. In pole-size koa, banana poka litter can comprise over 10% of the total fine litterfall and over 25% of the leaf litterfall. Poka litter can account for more the 30% of the nitrogen, phosphorus, and calcium returned to the forest floor in young stands, but less than 8% in mature stands and in lightly infested young stands. I conclude that banana poka is seriously affecting litterfall in portions of the predominantly native forest of Laupahoehoe.

Banana poka also has the potential to increase nutrient release from native detrital materials. A study is being planned to determine if the high nutrient content of poka litter and its apparent lack of organic compounds resistant to decay enhance decomposition of native leaf litters when they occur in mixture.

Based on estimated means and variances, sample sizes for future studies of litterfall and decomposition will be much larger, but probably not large enough to give a precision less than 20% of the mean, 95% of the time. Futhermore, decomposition studies must be conducted within pig-proof exclosures.

Acknowledgments

I thank Alan Urakami for his work in the establishment and field phases of these preliminary studies; Audrey Haraguchi for making the litter bags and helping to fill them; Janis Haraguchi for her painstaking separation of litter into component parts and subsequent drying, weighing, and recording; and Ernest Okazaki for doing the chemical analyses.

Literature Cited

Aber, John D. and Jerry M. Melillo. 1980. Litter decomposition: Measuring relative contributions of organic matter and nitrogen to forest soils. Can. J. Bot. 58:416-421.

Cromack, Kermit, Jr. and Carl D. Monk. 1975. Litter production, decomposition, and nutrient cycling in a mixed hardwood watershed and a white pine watershed. In: Mineral cycling in Southeastern ecosystems (F. G. Howell, J. B. Gentry and M. H. Smith, eds.), p. 609-624. ERDA Symposium Series (CONF-740513).

Division of Water and Land Development. 1982. Median rainfall, State of Hawaii. Circ. C88, Department of Land and Natural Resources, State of Hawaii.

Edwards, P. J. 1977. Studies of mineral cycling in a montane rain forest in New Guinea. II. The production and disappearance of litter. J. Ecol. 65:971-992.

Fogel, Robert and Kermit Cromack, Jr. 1977. Effect of habitat and substrate quality on Douglas fir litter decomposition in western Oregon. Can. J. Bot. 55:1632-1640.

Gerrish, Grant and Kent W. Bridges. 1984. A thinning and fertilizing experiment in Metrosideros dieback stands in Hawai'i. Univ. Hawaii, Hawaii Botanical Sci. Pap. No. 43., Department of Botany, Honolulu, Hawaii. 107 p.

Jensen, V. 1974. Decomposition of angiosperm tree leaf litter. In: Biology of plant litter decomposition, Vol. I (C. H. Dickinson and G. J. F. Pugh, eds.), p. 69-104. Academic Press, London.

Jones, R. C. and E. N. Okazaki. 1973. Plant tissue analysis by x-ray fluorescence quantometry. Agron Abstr., p. 8.

McClaugherty, C. A., John Pastor, and J. D. Aber. 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology 66:266-275.

McShane, M. C., D. W. Carlile, and W. T. Hinds. 1983. The effect of collector size on forest littre-fall collection and analysis. Can. J. For. Res. 13:1037-1042.

Melillo, Jerry, John D. Aber, and John F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621-626.

Smith, O. L. 1982. Soil microbiology: A model of decomposition and nutrient cycling. CRC Press, Inc., Boca Raton, Florida. 273 p.

Swift, M. J. O., O. W. Heal, and J. M. Anderson. 1979. Decomposition in terrestrial ecosystem. University of California Press, Berkeley, California.

Tanner, E. V. J. 1977. Mineral cycling in montane rain forests in Jamaica. Dissertation. Cambridge University, Cambridge, England.

Tanner, E. V. J. 1980. Litterfall in montane rain forests of Jamaica and its relation to climate. J. Ecology 68:833-848.

Tanner, E. V. J. 1981. The decomposition of leaf litter in Jamaican montane rain forests. J. Ecology 69:263-275.

Technicon Instrument Corporation. 1977. Individual/simultaneous determinations of nitrogen and/or phosphorus in BD acid digests. Industrial Method No. 329-74W. Tarrytown, N.Y.

Thaiutsa, Bunvong and Orman Granger. 1979. Climate and the decomposition rate of tropical forest litter. Unasylva 31:28-35.

Vitousek, Peter M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. Ecology 65:285-298.